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Acanthocephalans of the nominotypical subgenus of *Plagiorhynchus* (Plagiorhynchidae) from charadriiform birds in the collection of the Natural History Museum, London, with a key to the species of the subgenus

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Abstract

Specimens of three species of the nominotypical subgenus of *Plagiorhynchus* Lühe, 1911 (Acanthocephala, Plagiorhynchidae) are deposited in the Parasitic Worms Collection of the Natural History Museum, London. Two of these species are from birds collected in the United Kingdom: *Plagiorhynchus* (*Plagiorhynchus*) *crassicollis* (Villot, 1875) from *Charadrius hiaticula* L. and *P.* (*P.*) *odhneri* Lundström, 1942 from *C. hiaticula* and *Haematopus ostralegus* L. The third species, *P.* (*P.*) *charadrii* (Yamaguti, 1939), is from *Charadrius alexandrinus nihonensis* Deignan in the Pescadore Islands (near Taiwan). Since the morphology of the three species is poorly known, these specimens are described and figured and any variation is commented upon. A key to the species of the subgenus *Plagiorhynchus* is presented.

Keywords

Acanthocephala, *Plagiorhychus*, charadriiform birds, morphology, United Kingdom, Pescadore Islands, identification key

Introduction

Currently, 11 species of the nominotypical subgenus of *Plagiorhynchus* Lühe, 1911 (Acanthocephala, Plagiorhynchidae) are considered valid (Lisitsina 1992; Golvan 1994; Smales 2002). They are mainly parasitic in birds of the order Charadriiformes. The majority of the species are known on the basis of a few records only. Therefore,

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data on their variability are scarce. The aim of the present paper is to describe *Plagiorhynchus* (*Plagiorhynchus*) spp. from charadriiform birds deposited in the Parasitic Worms Collection of the Natural History Museum, London, in order to provide new data on their morphology, geographical distribution and host-range. In addition, an amended identification key to the species of the subgenus is presented.

Materials and methods

This study is based on acanthocephalans from the Parasitic Worms Collection of the Department of Zoology, Natural History Museum, London. In most cases, information on the fixation methods used is not available. The majority of the specimens have been stored in 80% ethanol. For the purposes of the present study, they were cleared in glycerine and water (25-100%) or dimethylphthalate and studied as temporary mounts. Other specimens have been preserved as whole-mounts in Canada balsam.

The descriptions are based on specimens from a single host specimen and thus one locality. Measurements are given in millimetres, unless otherwise indicated, as a range, with any individual measurements outside the normal range in parentheses.

The general distribution of host-species is given in accordance with Encyclopaedia Britannica Online (2009).

Results

***Plagiorhynchus* (*Plagiorhynchus*) *crassicollis* (Villot, 1875) Lühe, 1911**
Syn. *Plagiorhynchus lanceolatus* (von Linstow, 1876) Lühe, 1911

Material studied. BMNH 1928.2.17.91, from small intestine of *Charadrius hiaticula* L., Great Britain (detailed locality data not known), whole-mount of 2 specimens (1 slide) (material listed by Baylis, 1928); BMNH 1936.8.17.124-140, from small intestine of *C. hiaticula*, Weymouth, Dorset, England, wet material (material listed by Baylis 1939).

Description (Fig. 1)

Based on 10 male and 12 female specimens from *Charadrius dubius*, Weymouth, Dorset, England (BMNH 1936.8.17.124-140).

General. Trunk elliptical, almost ovoid, narrowing posteriorly. Transverse vessels of lacunar system form dense reticulum of large polygons. Proboscis cylindrical, situated at angle to axis of trunk. Proboscis armament consists of 19-20 longitudinal rows of 13-14 (12) hooks; first 8 (9) hooks longest, next 2 smaller and last 3 hooks smallest; all hooks with posteriorly directed roots. Neck short (partly or completely withdrawn in some specimens), trapezoidal. Proboscis receptacle double-walled. Lemnisci band-shaped (bifurcate in single specimen), longer than proboscis receptacle.

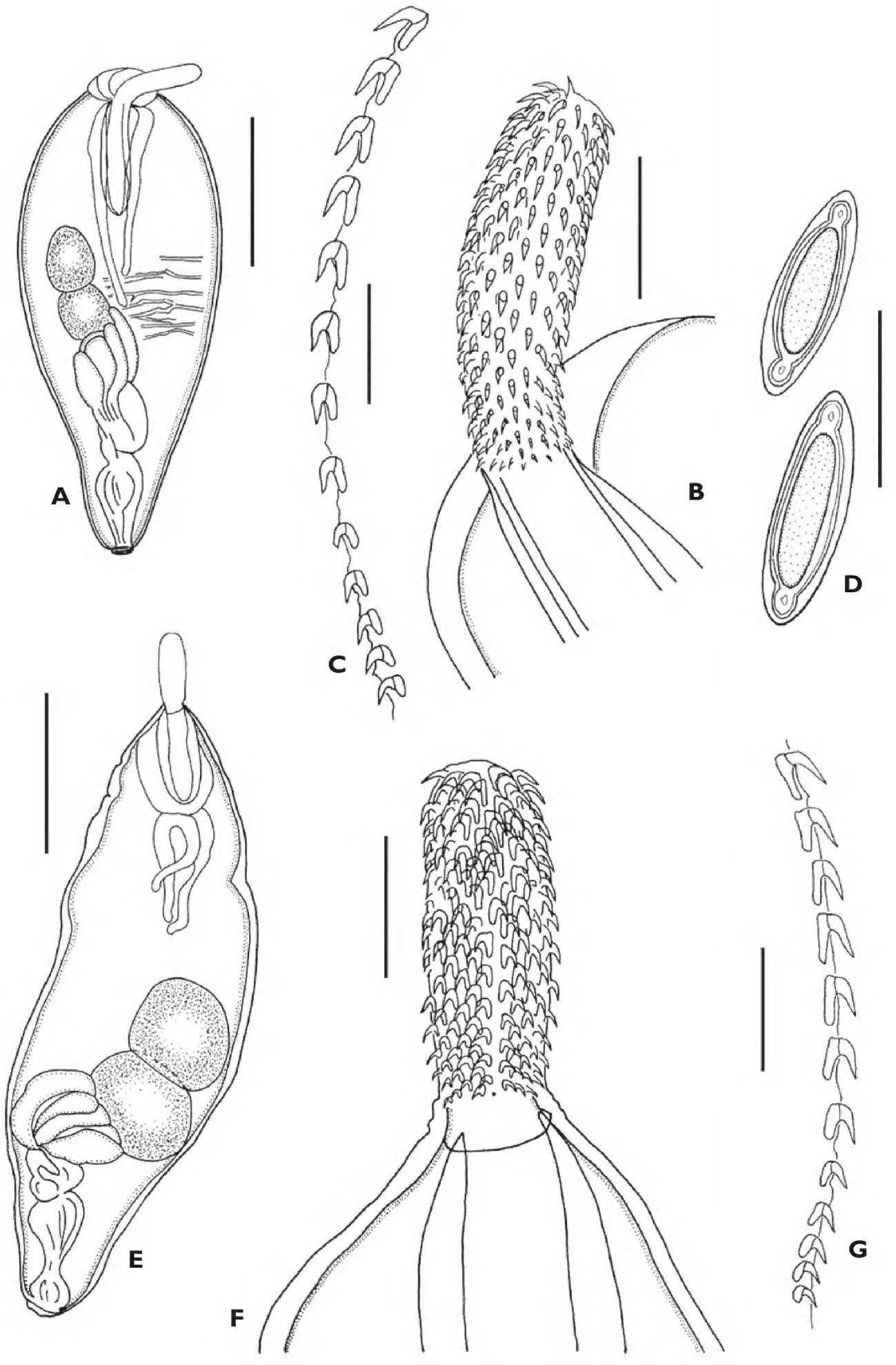

Fig. 1. *Plagiorhynchus* (*Plagiorhynchus*) *crassicollis* (Villot, 1875). **A-D** (material from Dorset): **A**. Male, general view. **B**. Male, anterior end of trunk. **C**. Male, longitudinal row of hooks (lateral view). **D**. Eggs. **E-G** (material from unknown locality, in Great Britain): **E**. Male, general view. **F**. Male, anterior end of trunk. **G**. Male, longitudinal row of hooks (lateral view). *Scale-bars*: A, E, 1.0 mm; B, F, 0.2 mm; C, D, G, 0.1 mm.

Male. Trunk 2.4-5.2 long, 1.0-1.64 wide. Proboscis (completely everted in only 2 specimens) 0.56-0.62 long, 0.16 wide. Length of first 8 hooks – blade 32-42 μm, root 32-44 μm; length of next 2 hooks – blade 29 μm, root 25-32 μm; length of last 3 hooks – 25-27 (29) μm, root 13-22 μm. Neck (in 2 specimens) *c.*0.1 long. Proboscis receptacle 0.70-0.95 long and 0.16-0.25 wide. Lemnisci 1.0-2.6 long, 0.09-0.15 wide. Testes oval to spherical, 0.30-0.80 long, 0.23-0.41 wide, situated in tandem and slightly overlapping one another, in middle region of trunk. Cement glands 6 in number, of different lengths, 0.30-0.95 long, situated immediately posterior to hind testis. Duct of cement glands 0.35-0.65 long. Genital bursa (everted in single specimen) 0.25 long, 0.30 wide.

Female. Trunk 2.64-7.0 long, 1.21-2.9 wide. Proboscis (completely everted in only 2 specimens) 0.66-0.7 long, 0.17-0.19 wide. Length of first 8 (9) hooks – blade 37-44 (49) μm, root 34-54 μm; length of next 2 hooks – blade 34-39 μm, root 27-39 μm; length of last 3 hooks blade – 17-29 μm, root 15-27 μm. Neck 0.15-0.17 long. Proboscis receptacle 0.72-1.1 long, 0.24-0.27 wide. Lemnisci 1.0-1.9 long, 0.1-0.13 wide. Female genital tract *c.*1.2-1.45 long. Vagina provided with 2 sphincters. Genital pore slightly subterminal, at 0.06-0.12 from posterior end of trunk. Fully-developed eggs were observed in 4 specimens (5.1-7.0 long). Eggs elongate-oval, shuttle-shaped, with polar prolongations, 91-134 (135) × 25-42 μm.

Additional data. (based on 2 male specimens from *C. hiaticula*, BMNH 1928.2.17.91). Trunk 4.0-4.7 in length, 1.4-1.55 wide. Proboscis 0.48-0.5 long. Proboscis armament consists of 20 longitudinal rows of 11-12 hooks in each row. Measurements and morphology of hooks are similar to material from Dorset. Neck very short (40-63 μm long). Testes spherical, 0.60-0.65 long, 0.75-0.87 wide. Cement glands 0.55-1.0 long.

Remarks. There are only a few descriptions of this species (Lühe 1911; Petrochenko 1958; Belopol'skaya 1983; del Valle and Coy Otero 1990). Only female specimens were described by Petrochenko (1958) from *Phalaropus lobatus* (L.) [= *P. hyperboreus* (L.)] in Kazakhstan. Compared to previous descriptions of the same species (Lühe 1911; Belopol'skaya 1983), the specimens from Kazakhstan differ in the shape and the length of the trunk (elongate-cylindrical and 17 mm long versus oval and *c.*7 mm long), the shape of the proboscis (oval versus cylindrical) and the number of longitudinal rows of hooks (16 longitudinal rows of hooks versus 18-20). In addition, there are differences in the dimensions of the eggs: 84 × 16 μm (Petrochenko 1958) versus 110 × 49 μm (Lühe 1911). Consequently, it seems likely that the specimens from Kazakhstan described by Petrochenko (1958) belong to another species.

Del Valle and Coy Otero (1990) reported *P. crassicollis* from *Charadrius wilsonia wilsonia* Ord in Cuba. According to their description, the armature of the proboscis consists of 18 longitudinal rows of 10-11 hooks per row. However, judging by the drawing of the proboscis (figure 1c in del Valle and Coy Otero 1990), the number of hooks per row is at least 18.

Comparing the morphometric data of the present specimens with the descriptions of Lühe (1911) and Belopol'skaya (1983), there are several differences. The maximum

number of hooks per longitudinal row in the specimens studied is greater, i.e. 11-14 versus 11-12 (Lühe 1911) or 13 (Belopol'skaya 1983). The male specimens among our material (see 'Additional data' above) are in close accordance with the description of Lühe (1911); however, they have a smaller proboscis, i.e. 0.48-0.50 versus 0.60 mm. A difference in the females relates to the size of eggs, which are larger in our specimens, i.e. 91-134 × 25-42 µm compared to 110 × 49 µm (Lühe 1911) and 88-102 × 27-34 µm (del Valle and Coy Otero 1990).

One immature female from the same host specimen (Dorset material) possesses a longer proboscis (0.76 mm) and a greater number of hooks per row (15-16). According to these characters, we consider it as belonging to *Plagiorhynchus odhneri* Lundström, 1942 (see 'Additional data' for *P. odhneri*).

P. (*P.*) *crassicollis* was previously reported from *Charadrius hiaticula* (= *Aegialitis hiaticula*) in the United Kingdom (Baylis 1928, 1939), once apparently in a mixed infection with *P. odhneri* (see below). It is mainly a parasite of charadriiform birds throughout the western Palaearctic [(Germany, France, Sweden, Switzerland, Ukraine, Russia (the White and Baltic Sea coasts)] (Lühe 1911; Belopol'skaya 1983; Hansson 1997; Reimer 2002; Gibson 2004). There are also occasional records from the Nearctic [Greenland (Hansson 1997)] and Neotropical [Cuba (del Valle and Coy Otero 1990)] Regions.

Plagiorhynchus (*Plagiorhynchus*) *odhneri* Lundström, 1942

Material studied. [All labelled as *P. crassicollis*.] BMNH 1946.5.14.121-122, from small intestine of *Charadrius hiaticula*, Orkney Islands, Scotland, wet material (3 specimens); BMNH 1936.8.17.124-140 (1 immature female), from small intestine of *C. hiaticula*, Weymouth, Dorset, England, wet material; BMNH 1951.12.12.34, from small intestine of *Haematopus ostralegus* Linnaeus, Holy Island (adjacent to Isle of Arran), Scotland, wet material (1 specimen).

Description (Fig. 2)

Based on 1 male and 1 female specimen and 1 metasoma (female) from BMNH 1946.5.14.121-122.

Male. Length of trunk (deformed) 4.0. Proboscis cylindrical, situated at angle to trunk axis, 0.68 long, 0.15 wide. Proboscis armament consists of 20 longitudinal rows of 16-17 hooks per row. Length of first 9 (10) hooks – blade 32-42 µm, root 34-37 µm; length of next 3 hooks – blade 25-27 µm, root 25-34 µm; length of last 3 hooks – blade 22 µm, root 15-20 µm. Neck trapezoidal, 0.18 long, 0.13-0.22 wide. Proboscis receptacle 0.6 long, 0.2 wide. Lemnisci 1.3 (1.4) long, 0.1-0.11 wide. Testes not clearly seen; anterior testis at *c.*1.12 from tip of proboscis receptacle. Length of cement glands *c.*0.80.

Female. Trunk elliptical, oval to fusiform, 4.4-5.6 long, 1.9-2.2 wide. Proboscis cylindrical, situated at angle to trunk axis, 0.76 long, 0.19 wide. Proboscis armament consists of 17 longitudinal rows of 15-16 hooks per row. Length of first 9 (10) hooks – blade 37-49 µm, root indistinct; length of next 2-3 hooks – blade 29-32 µm, root indistinct; remaining 4 hooks could not be measured. Neck withdrawn. Proboscis re-

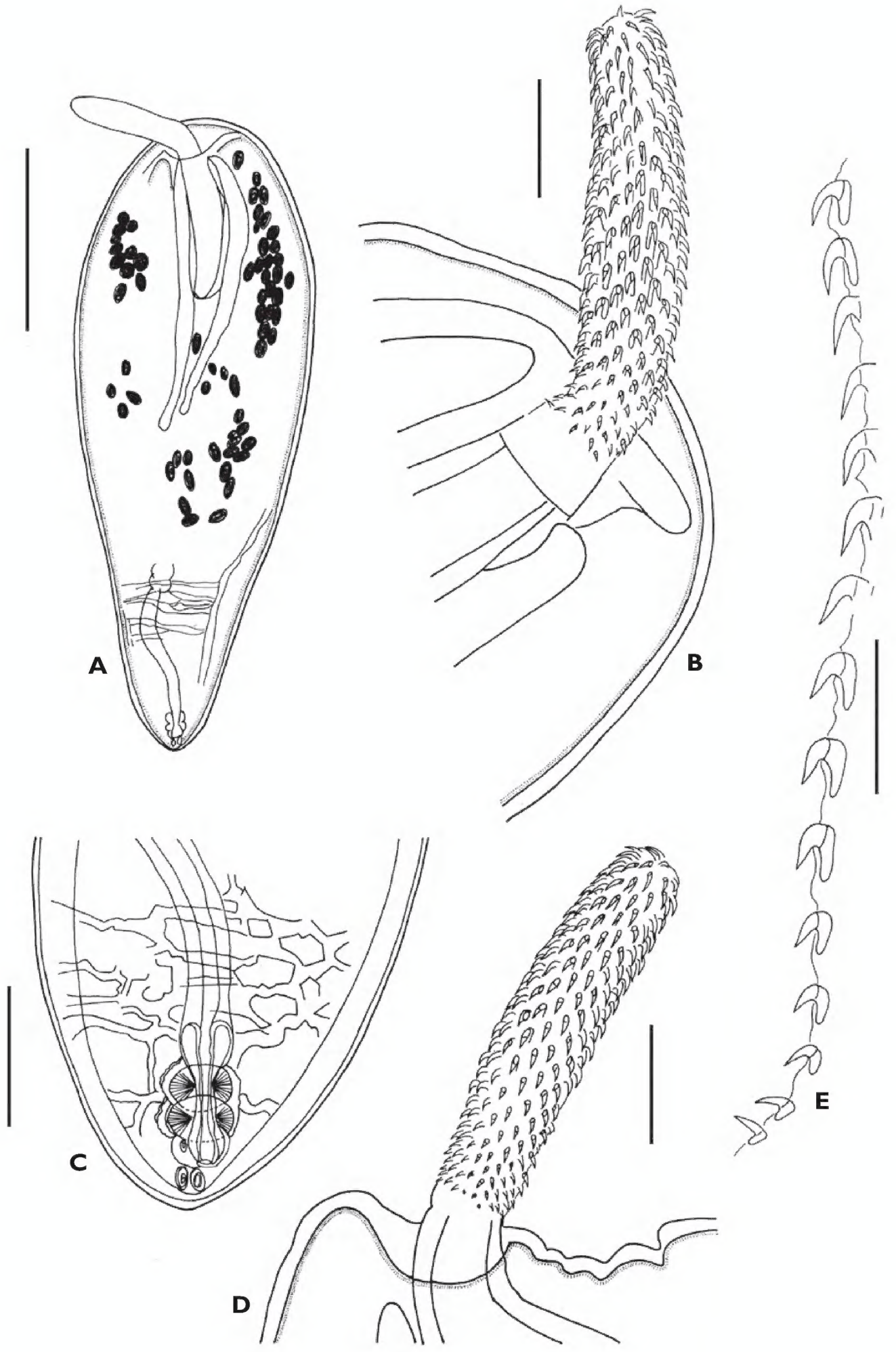

Fig. 2. *Plagiorhynchus* (*Plagiorhynchus*) *odhneri* Lundström, 1942. **A**. Female, general view. **B**. Female, anterior end of trunk. **C**. Female, posterior end of trunk with terminal genital tract. **D**. Male, anterior end of trunk. **E.** Female, longitudinal row of hooks (lateral view). *Scale-bars*: A, 1.0 mm; B, C, D, 0.2 mm; E, 0.1 mm.

ceptacle and lemnisci indistinct. Genital pore at 0.2 from end of trunk. Eggs elongate-oval, shuttle-shaped, with polar prolongations, 93-115 × 20-39 µm.

Additional data. Based on 1 immature specimen from *C. hiaticula* and 1 specimen from *Haematopus ostralegus*. Trunk of immature specimen 3.6 long, 1.4 wide. Proboscis cylindrical, situated at angle to trunk axis, 0.76 long, 0.17 wide. Proboscis armament consists of 18 longitudinal rows of 15-16 hooks in each row. Length of first 9-10 hooks – blade 36-43 µm, root 39-44 µm; length of next 2-3 hooks – blade 27-32 µm, root 27-39 µm; length of last 3 hooks 22-27 µm, root 20 µm (for hooks XIV-XV). Trunk of female specimen *c.*4.0 long, 1.55 wide. Proboscis 0.8 long, 0.15 wide.

Remarks. Lundström (1942) described this species from *Haematopus ostralegus* in Sweden. Golvan (1956) considered it to be a variety of *P. crassicollis* and later (Golvan 1960) as a subspecies. In the taxonomic arrangement of the nominotypical subgenus of *Plagiorhynchus* proposed by Schmidt and Kuntz (1966) and Amin (1985), this species is missing. According to other authors (Petrochenko 1958; Yamaguti 1963; Khokhlova 1986; Golvan 1994), *P. odhneri* is a valid species. Lisitsina (1992) redescribed it on the basis of specimens from *Charadrius dubius* Scopoli and *C. alexandrinus* L. in the Ukraine.

Unfortunately, the type material of this species was not available for re-examination during the course of the present study. The studied specimens were identified as *P. odhneri* mainly on the basis of the proboscis armature (especially with regard to the number of hooks in each longitudinal row). The armature (17-20 longitudinal rows of 15-17 hooks) recorded in the present study is within the limits of variation reported by Lundström (1942) in the original description (18-19 longitudinal rows of 14-18 hooks) and by Lisitsina (1992) (18-22 longitudinal rows of 15-19 hooks).

In comparison with the previous descriptions (Lundström 1942; Lisitsina 1992), I found some differences. These mainly concern the shape and measurements of the trunk. The present specimens possess an almost oval trunk (only the female metasoma is spindle-shaped) with measurements of 4.0 × ? (male) and 4.4-5.6 × 1.9-2.2 mm (female) versus an almost spindle-shaped trunk measuring 5.0-8.4 × 0.8-1.7 (male) and 9.0-11.0 × 1.7-2.4 mm (female), as described by Lundström (1942), and an almost cylindrical trunk measuring 3.57-6.58 × 0.96-1.58 (male) and 8.76-12.53 × 1.10-1.23 mm (female), according to Lisitsina (1992). With regard to these characters, our specimens are close to *P. crassicollis* (see above), as described by Lühe (1911), with an oval trunk and measurements of 5.0 × 1.6-1.8 (male) and 7.0 × 3.0 mm (female).

In addition, the proboscis of our worms is shorter, i.e. 0.68 (male) and 0.76-0.8 mm (female) compared with 0.8 (male) and 0.9-1.1 mm (female) as recorded by Lundström (1942). However, it is longer than the proboscis of *P. crassicollis* (0.6 mm) (Lühe 1911). Lisitsina (1992) reported wider limits of variation for this character (0.68-1.23 mm in both sexes), and our specimens fit within this morphometric range. More abundant material is needed to assess the variation within *P. odhneri* and to confirm its validity.

P. odhneri has previously been reported from *Charadrius hiaticula* and *Haematopus ostralegus* in the United Kingdom (Williams 1961; Threlfall 1963). Other records are from charadriiform birds in Sweden, Russia (White Sea coast), the Ukraine and Bulgaria (Lundström 1942; Belopol'skaya 1983; Lisitsina 1992; Hansson 1997; Dimitrova et al. 2000).

***Plagiorhynchus* (*Plagiorhynchus*) *charadrii* (Yamaguti, 1939) Van Cleave & Williams, 1951**

Material studied. BMNH 1965.931-937, from the small intestine of *Charadrius alexandrinus nihonensis* Deignan, Pescadore Islands, Taiwan, whole-mount of 2 specimens (1 slide).

Description (Fig. 3)

Based on 2 male specimens.

Males. Trunk elongate, almost cylindrical but tapering both anteriorly and posteriorly, 3.7-4.0 long, 0.9-1.1 wide. Numerous amoeba-shaped hypodermal nuclei. Proboscis cylindrical (in both specimens invaginated to different degrees, i.e. anterior third in first specimen and anterior two-thirds in other), *c*.0.93-0.95 long, 0.23 wide. Proboscis armament consists of 18 longitudinal rows of 12-13 hooks (anterior hooks invaginated) (in 1 specimen). Most of hooks with posteriorly directed roots; only pos-

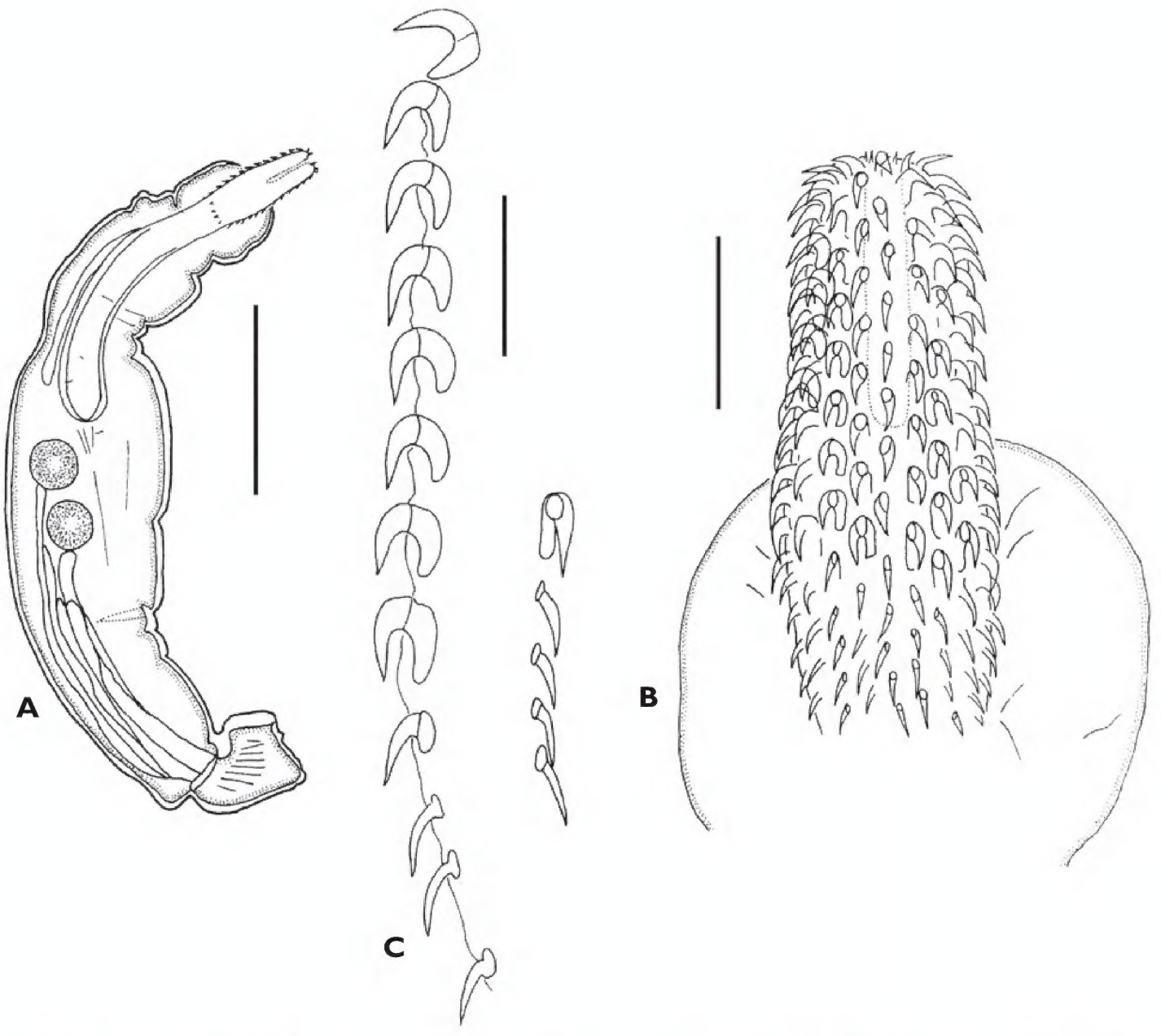

Fig. 3. *Plagiorhynchus* (*Plagiorhynchus*) *charadrii* (Yamaguti, 1939). **A**. Male, general view. **B**. Proboscis. **C**. Longitudinal rows of hooks (lateral view) and some posterior hooks (frontal view). *Scale-bars*: A, 1.0 mm; B, 0.2 mm; C, 0.1 mm.

teriormost 4 (3) hooks spiniform with short apophyses. Length of first 8 (9) hooks – blade 52-59 µm, root 29-49 µm; length of last 4 (3) spiniform hooks – 42-52 (54) µm, root 12-22 µm. Neck short, *c.*0.13 long, 0.25 wide. Proboscis receptacle double-walled, 1.5 long, 0.26 wide. Lemnisci band-shaped, *c.*1.5 long, *c.*0.05 wide (only 1 measured). Testes spherical, 0.26-0.32 long, 0.23-0.35 wide, situated in tandem in middle of trunk, at *c.*0.06 from one another; anterior testis 0.14 from tip of proboscis receptacle. Cement glands 6 in number, tubular, arranged in 2 groups of 3; longest cement gland of first group (1.70 long) present immediately posterior to anterior testis; remaining 2 cement glands slightly further posterior, 1.44 and 1.01 long; 2 of cement glands of second group present posterior to hind testis, 1.35 long, with remaining cement gland slightly further posterior, 1.03 long. Genital bursa (everted in 1 specimen) 0.55 long, 0.45 wide.

Remarks. Despite the partial invagination of the proboscis, we identified these specimens as *Plagiorhychus charadrii* based on the number of the longitudinal rows and morphometric data from both the hooks (especially the posterior three or four hooks) and of some internal organs (testes and cement glands). When comparing the present morphometric data with those from published descriptions (Yamaguti 1939; Johnston and Edmonds 1947; Schmidt and Kuntz 1966; Belopol'skaya 1983; Amin et al. 1999; Dimitrova et al. 1999), we did not find significant differences, although differences in the maximum length of the hook blade are apparent. Regarding the latter feature, the studied specimens are most similar to the descriptions given by Yamaguti (1939), Schmidt and Kuntz (1966) and Dimitrova et al. (1999), i.e. 60-63 versus 59 µm in present specimens. However, Johnston and Edmonds (1947) and Belopol'skaya (1983) reported smaller lengths for the hooks, i.e. 29 and 54 µm, respectively.

This species was described from *Charadrius dubius curonicus* Gmelin in Japan (Yamaguti 1939) and later recorded, mainly from charadriiform birds, in the Australian Region (Australian mainland and Tasmania) (Johnston and Edmonds 1947; Amin et al. 1999; Smales 2002, 2003), the Palaeotropical Region (Taiwan and the Pescadore Islands) (Schmidt and Kuntz 1966; Amin et al. 1999), the Palaearctic Region (Japan, Russian Far East, Kazakhstan, the Ukraine and Bulgaria) (Lisitsina 1992; Amin et al. 1999; Dimitrova et al. 1999; Araki 2003), the Oceanic Region (Hawaii) (Amin et al. 1999) and the Neotropical Region (Belize) (Canaris and Kinsella 2001).

Discussion

The most recent checklist of the species of the subgenus *Plagiorhynchus* is that given by Golvan (1994). He considered *Plagiorhynchus* and *Prosthorhynchus* as distinct genera (recognised here as subgenera within *Plagiorhynchus*) and placed 19 species in the former. In my opinion, nine of them do not belong to the subgenus *Plagiorhynchus*. These are:

P. kuntzi Gupta & Fatma, 1987. Gupta and Fatma (1987) described this species as a member of *Plagiorhynchus* on the basis of specimens collected from *Buceros bicornis* L. [= *Dichoceros bicornis* (L.)] in India. The authors presented ambiguous information

relative to the two main features distinguishing the subgenera *Plagiorhynchus* and *Prosthorhynchus*, i.e. "eggs with and without polar prolongations" and "female gonopore terminal or subterminal". Furthermore, the host is a forest bird, eating mainly fruit. Therefore, the position of this species remains uncertain and it cannot be allocated to the subgenus *Plagiorhynchus*.

P. limnobaeni (Tubangui 1933) Van Cleave & Williams, 1951. Tubangui (1933) described this species on the basis of two male specimens and placed it in *Prosthorhynchus*. Van Cleave and Williams (1951) transferred it to *Plagiorhynchus*. Golvan (1956) considered it also in *Plagiorhynchus*. However, Petrochenko (1958), Yamaguti (1963), Schmidt and Kuntz (1966) and Amin (1985) considered it to belong to *Prosthorhynchus*, and Amin et al. (1999) included it in their key to the species of the subgenus *Prosthorhynchus* on the basis of the proboscis armature. Unfortunately, the known features of the male specimens only are not adequate to confirm the validity of this species or its position within the subgenus *Plagiorhynchus*.

P. pupa (von Linstow, 1905) Golvan, 1994. Kostylev (1922) redescribed this species on the basis of materials from *Somateria molissima* L. as *Echinorhynchus pupa*. Travassos (1926) transferred it to *Filicollis* Lühe, 1911, but Meyer (1932) proposed it be attributed to *Prosthorhynchus*. Nevertheless, Petrochenko (1958) listed it among the species of *Polymorphus* as "*Polymorphus pupa* (von Linstow, 1905) Kostylew, 1922". This generic allocation was followed by Khokhlova (1986) and Amin (1992). According to the ICZN, the valid combination for this species is *Polymorphus pupa* (von Linstow, 1905) Petrochenko, 1958.

P. rectus (Linton, 1892) Van Cleave, 1918. The original description was based on one male and one immature female (Van Cleave 1918). Van Cleave (1918) re-examined the female specimen but did not give any details of the female genital system (except mentioning that there were no ripe eggs). Its position in *Prosthorhynchus* has been accepted by many authors (e.g. Travassos 1926; Meyer 1932; Petrochenko 1958; Amin 1985), but Schmidt and Kuntz (1966) considered it as a *species incertae sedis*. This species was recorded from an aquatic host (*Larus* sp.). The inadequate description of females does not permit its consideration as a species of the subgenus *Plagiorhynchus*.

P. reticulatus (Westrumb, 1821) Golvan, 1956. This species was recorded from aquatic birds (Rallidae and Charadriidae) from Brazil. De Marval (1905) described the presence of polar prolongations of eggs, whereas Travassos (1926) reported eggs without polar prolongations. It is almost generally accepted that this species belongs to the subgenus *Prosthorhynchus* (see Meyer 1932; Petrochenko 1958; Yamaguti 1963; Schmidt and Kuntz 1966; Amin 1985; Amin et al. 1999).

P. rostratus (De Marval, 1902). De Marval (1905) considered this species as a synonym of '*Echinorhynchus cylindraceus* Schrank, 1788'. Meyer (1932), Petrochenko (1958) and Yamaguti (1963) recognised it as *Prosthorhynchus rostratus,* whereas Golvan (1956) and Schmidt (1981) listed it among the synonyms of *Plagiorhynchus* (*Prosthorhynchus*) *cylindraceus* (Goeze, 1782) Schmidt & Kuntz, 1966. Amin (1985) recognised this species among the Plagiorhynchinae *incertae sedis*. Data on the eggs and female genital system are not available, but the hosts are terrestrial birds (Corvidae).

The position of this species is uncertain, but the most probable allocation on the basis of the available data is to the subgenus *Prosthorhynchus*.

P. spiralis (Rudolphi, 1809) Golvan, 1956. Schmidt and Kuntz (1966) considered this as a *species incertae sedis*. Amin (1985) recognised it as valid species within the subgenus *Plagiorhynchus*. However, Dimitrova and Georgiev (1994) examined both the type material and new material from Bulgaria and erected for it the monotypic *Ardeirhynchus* Dimitrova and Georgiev, 1994 (Polymorphidae) due to the presence of trunk spines.

P. taiwanensis Schmidt & Kuntz, 1966. According to Schmidt (1981), Amin (1985) and Amin et al. (1999), this species is a synonym of *Prosthorhynchus cylindraceus* (Goeze, 1782).

P. urichi (Cameron, 1936) Golvan, 1956. This species was described from *Procyon ?carnivora* (probably *P. lotor* L.) in Canada (Yamaguti 1963). Except for Golvan (1956, 1994), only Yamaguti (1963) considered it as a valid species, but placed it in *Prosthorhynchus*. Both Schmidt and Kuntz (1966) and Amin (1985) considered it as *Plagiorhynchus incertae sedis* and Plagiorhynchinae *incertae sedis*, respectively, due to its inadequate description.

'P. freitasi Vicente, 1977'. Golvan (1994) listed this species in his list of *Plagiorhynchus* spp, but did not cite the source. There is no record of this taxon in the *Zoological Record*.

Two further species are not included in Golvan's (1994) checklist. These are *Plagiorhynchus ponticus* Lisitsina, 1992, a parasite of *Haematopus ostralegus* L. (Charadriiformes, Haematopidae) in the Ukraine (Lisitsina 1992), and *P. allisonae* Smales, 2002 from *H. ostralegus finschi* Martens in New Zealand (Smales 2002). Therefore, a total of 11 species are considered here as belonging to the subgenus *Plagiorhynchus,* and these are included in the key presented below.

According to Schmidt and Kuntz (1966), there are two main characters distinguishing the subgenera *Plagiorhynchus* and *Prosthorhynchus* from one another. These are the terminal position of the female genital pore and the elongate eggs with prolongations of the middle shell (in *Plagiorhynchus*) *versus* the subterminal female genital pore and the oval eggs without polar prolongation (in *Prosthorhynchus*). However, in two of the species included in the subgenus *Plagiorhynchus*, the genital pore is subterminal, i.e. in *P. ponticus* (Lisitsina 1992) and *P. paulus* Van Cleave & Williams, 1951 (see Amin et al. 1999). In addition, Dimitrova et al. (1999) and the present study described a slightly subterminal genital pore in *Plagiorhynchus charadriicola* (Dollfus, 1953) Golvan, 1956, *P. crassicollis* and *P. odhneri*; all of which are characterised by a vagina possessing two sphincters. Belopol'skaya (1983) reported slightly a subterminal pore and vagina with two sphincters in *Prosthorhynchus scolopacidis* Kostylev, 1915. In order to increase the usefulness of these characters, more data of the structure of the vagina will be required in future studies. It seems that the position of the genital pore correlates with the structure of the vagina, e.g. the genital pore of *Prosthorhynchus cylindraceus* is distinctly subterminal and the vagina (with one sphincter) is curved, forming angle (Amin et al. 1999; Dimitrova et al. 1999), whereas, in other species (*Plagiorhynchus charadriicola*, *P. crassicollis* and *P. odhneri*), the vagina is straight, provided with two sphincters and the genital pore is terminal or slightly subterminal.

Both Johnston and Best (1943) and Smales (2002) redescribed *Plagiorhynchus menurae* Johnston, 1912 and reported the nerve ganglion as positioned at the posterior end of the proboscis receptacle. However, according to Lühe (1911) and Schmidt and Kuntz (1966), the position of this ganglion is about the middle of the proboscis receptacle for species of the genus *Plagiorhynchus*.

Key to the species of the *Plagiorhynchus* (*Plagiorhynchus*)

1 Trunk elongate-cylindrical, linear, up to 50-80.7 mm long **2**
– Trunk shorter (up to 30 mm), with different shape **3**

2 Trunk up to 50 mm long; proboscis with 18 longitudinal rows of 12-18 hooks per row (in Charadriiformes: Europe) ..... ***P. linearis* (Westrumb, 1821) Golvan, 1956**
– Trunk up to 80.7 mm long; proboscis with 24 longitudinal rows of 18 hooks per row (in Charadriiformes: Europe) ..... ***P. totani* (Porta, 1910) Golvan, 1956**

3 Female genital pore distinctly subterminal **4**
– Female genital pore terminal or slightly subterminal **5**

4 Trunk smooth; proboscis with 15-16 longitudinal rows of 14-16 hooks per row; eggs 50-82 µm long (in Passeriformes: North America) ..... ***P. paulus* Van Cleave & Williams, 1951**
– Trunk with pseudosegmentation; proboscis with 20-25 longitudinal rows of 16-17 hooks per row; eggs 118-130 µm long (in Charadriiformes: Ukraine) ..... ***P. ponticus* Lisitsina, 1992**

5 Maximum length of proboscis up to 1.23 mm, with 16-23 longitudinal rows of 11-20 hooks per row; nerve ganglion in middle region of proboscis receptacle **6**
– Proboscis longer (1.8-2.58 mm long), with 25-26 longitudinal rows of 30-38 hooks per row; nerve ganglion in posterior region of proboscis receptacle (in Passeriformes: Australia) ..... ***P. menurae* (Johnston, 1912) Golvan, 1956**

6 Trunk ovoid to fusiform; maximum length of hooks 44-45 µm; last 1-5 hooks spiniform, with posteriorly directed roots **7**
– Trunk fusiform to subcylindrical; maximum length of hooks 50-65 µm; last 2-6 hooks spiniform, sometimes with manubrium **8**

7 Trunk ovoid; proboscis 0.6-0.7 mm long, with 18-20 longitudinal rows of 11-14 hooks per row (in Charadriiformes: Europe) ..... ***P. crassicollis* (Villot, 1875) Lühe, 1911**

– Trunk elongate-fusiform; proboscis 0.8-1.23 mm long, with 17-22 longitudinal rows of 14-19 hooks per row (in Charadriiformes: Europe)..... ..... ***P. odhneri*** **Lundström, 1942**

8 Trunk subcylindrical; proboscis with 16-20 longitudinal rows of 15-19 hooks per row; lemnisci 3.0-5.1 mm long; eggs 90-120 µm long **9**

– Trunk fusiform; proboscis with 18-23 longitudinal rows of 14-20 hooks per row; lemnisci 1.1 mm long; eggs 134-154 µm long (in Charadriiformes: New Zealand) ..... ***P. allisonae*** **Smales, 2002**

9 Females 8.0 mm long; lemnisci 5.1 mm long (in Charadriiformes: Russia)... ..... ***P. lemnisalis*** **Belopol'skaya, 1958**

– Females longer than 10 mm; lemnisci 3.0-4.5 mm long..... **10**

10 Males 9.6 mm long, females 11.5 mm long;15-19 hooks per row; last 3-4 hooks without root or with short anterior manubrium; genital pore on a caudal nodule (in Charadriiformes; Asia, Europe, Australia, Central America)... .....***P. charadrii*** **(Yamaguti, 1939) Van Cleave & Williams, 1951**

– Males 9-13 mm long, females 17-23 mm long; 15-17 hooks per row; last 2-3 hooks with rectangular root with anterior and posterior manubrium; genital pore not on a caudal nodule (in Charadriiformes: Morocco, Europe) ....*P. charadriicola* **(Dollfus, 1953) Golvan, 1956**

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